

1 Running head: Evolutionary responses to conditionality

2 Evolutionary responses to conditionality in species interactions across environmental gradients

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12 Statement of authorship: AO and SYS contributed to the development of the hypothesis. All au-
13 thors contributed to the revising of the manuscript. AO proposed the hypothesis and provided the
14 first draft of the manuscript.

15 Submitted as an Article to the American Naturalist

16 Word counts: Abstract-207 Main-5550

17 4 figures. No tables, supplemental files, or text boxes.

18 Number of references: 93

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Abstract

The outcomes of many species interactions are conditional on the environments in which they occur. A common pattern is that outcomes grade from being more positive under stressful conditions to more antagonistic or neutral under benign conditions. The evolutionary implications of conditionality in interactions have received much less attention than the documentation of conditionality itself, with a few notable exceptions. Here, we predict patterns of adaptation and co-adaptation between partners along abiotic gradients, positing that when interactions become more positive in stressful environments, fitness outcomes for mutations affecting interactions align across partners and selection should favor greater mutualistic adaptation and co-adaptation between interacting species. As a corollary, in benign environments, if interactions are strongly antagonistic, we predict antagonistic co-adaptation resulting in Red Queen or arms-race dynamics, or reduction of antagonism through character displacement and niche partitioning. We predict no adaptation if interactions are more neutral. We call this the CoCoA hypothesis: **(Co)**-adaptation and **Co**nditionality across **A**biotic gradients. We describe experimental designs and statistical models that allow testing predictions of CoCoA, with a focus on positive interactions. While only one study has included all the elements to test CoCoA, we briefly review the literature and summarize study findings relevant to CoCoA and highlight opportunities to test CoCoA further.

Keywords: *biotic interactions, mutualism, local adaptation, co-adaptation, environmental gradients*

50 **Outcomes of biotic interactions depend on abiotic conditions**

51 The fitness impacts of biotic interactions are shaped by the conditions in which they occur. For
52 example, warming temperatures cause corals to expel their zooxanthellae symbionts (Hoegh-
53 Gulberg, 1999), increasing fire frequency and severity favors invasive over native grasses in
54 competitive interactions (D'Antonio and Vitousek, 1992), and predation on pepper moths is al-
55 tered by the prevalence of air pollution (Kettlewell, 1955). Conditionality in mutualisms is also
56 well known (Cushman and Whitham, 1989; Bronstein, 1994), and a meta-analysis of mutualism
57 studies finds that mutualistic outcomes are variable across space and habitats (Chamberlain et al.,
58 2014).

59 Two well-developed and related models of species interactions seek to predict changing fit-
60 ness impacts of biotic interactions for partners (interaction outcomes) across gradients. First,
61 economic models of mutualism describe inequalities with respect to resources and predict con-
62 ditional outcomes from true mutualistic outcomes (both species receive fitness benefits, or +,+
63 outcomes) to antagonism (+,- or -,- fitness outcomes). When the resources a participant *receives*
64 in trade from partners are those that are most limiting to the participant's fitness, the benefits from
65 trading are maximized; when resources the participant *provides* to partners limit the participant's
66 fitness, the costs of engaging in trade are maximized (Johnson, 1993; Schwartz and Hoeksema,
67 1998; Bever, 2015). Resource-based conditionality has been shown to exist for many "mutu-
68 alisms" (Bronstein, 1994), for example between plants and mycorrhizal fungi, which typically
69 provide soil nutrients to plants in exchange for carbon. This exchange benefits plants in low nu-
70 trient (stressful) conditions, but often imposes costs when nutrient availability is high (Smith
71 et al., 2010).

72 A second model closely tied to environmentally conditional outcomes in species interactions
73 is the Stress-Gradient hypothesis (SGH). The SGH posits that the relative importance of costs
74 and benefits from biotic interactions changes across stress gradients (Bertness and Callaway,
75 1994), and that interactions will gradually shift from having neutral or negative outcomes un-
76 der benign abiotic conditions to having beneficial outcomes under stressful conditions (Brooker

77 and Callaghan, 1998; Malkinson and Tielbörger, 2010). In some cases, plants are mutualistic as
78 seedlings in stressful conditions, but are less affected by these stresses as adults, and they then
79 compete (Sthultz et al., 2007). In other cases, stresses may be sufficiently great that the positive
80 interactions between species are maintained through the lifecycle. For example, stressful high
81 altitude conditions often result positive interactions between species that are positive through-
82 out life (Sthultz et al., 2007; He et al., 2013). For the purposes of this paper, we consider cases
83 in which the conditionality of abiotic stress is either consistent over the lifetime of an interaction
84 (e.g., seedling to adult), or we simplify to the net fitness effects of the interaction. In other words,
85 if seedlings of different species facilitate each other, and seedling mortality has the greatest ef-
86 fects on fitness, then, even if adults compete, we would consider the interaction under stress as
87 positive. A meta-analysis of SGH in plants found consistent shifts towards facilitation (0,+) or
88 reduced competition (0,- or -,- with smaller fitness effects) at high stress (He et al., 2013).

89 These separate theories are united by a focus on change in interaction benefits over abiotic
90 gradients: when interactions ameliorate fitness-limiting factors, they are expected to have posi-
91 tive effects on fitness, and when they exacerbate fitness-limiting factors, they should decrease fit-
92 ness. The theories use different language for overlapping concepts (“stress”, “limiting resources”).
93 Here, we use “stress” to describe this overlap: an abiotic condition that limits fitness. The SGH
94 and resource-based conditionality were originally detailed to explain changes from competi-
95 tion to facilitation in plant interactions and changes from mutualism to antagonism in plant-
96 microbe interactions, respectively, yet they have been applied to a diversity of interactions such
97 as detritivore-detritivore (Fugère et al., 2012), herbivore-herbivore (Dangles et al., 2013), plant-
98 herbivore (Daleo and Iribarne, 2009), and bacterial cross-feeding (Hoek et al., 2016), all of which
99 become increasingly facilitative or decreasingly costly as a stress the interaction ameliorates in-
100 creases.

101 The evolutionary implications of conditionality in interactions have received much less atten-
102 tion than the documentation of conditionality itself, with notable exceptions (Schwartz and Hoek-
103 sema, 1998; Thompson, 2005; Bronstein, 2009; Michalet et al., 2011). The geographic mosaic

104 theory of coevolution (GMTC, Thompson, 2005) suggests that as fitness consequences of inter-
105 actions vary across space, selection pressure from these variable interactions will result in dif-
106 ferent evolutionary outcomes. The GMTC is well supported (Thompson, 2005; Schemske et al.,
107 2009), yet lacks a framework for linking characteristics of the environment to specific evolution-
108 ary outcomes.

109 Here, we generalize these predictive frameworks for species interaction outcomes and unite
110 them with evolutionary principles. Our hypothesis links effects of limiting gradients on interac-
111 tion outcomes to the degree of adaptation to species interactions in pairs of populations across
112 stress gradients. We first leverage existing theory of conditionality, stress gradients, and geo-
113 graphic mosaics to generate predictions, then propose experimental and analytical methods for
114 testing this hypothesis and discuss existing relevant literature.

115 **Evolutionary responses to conditionality: a hypothesis**

116 Because conditionality models predict that environmental or resource gradients result in pre-
117 dictable variation in interaction outcomes, we suggest that evolution in these contexts might
118 also result in predictable outcomes. Extending the predictions of conditionality in interaction
119 outcomes to coevolutionary dynamics, we predict selection should result in adaptation and co-
120 adaptation in species interactions that are shaped by environmental gradients.

121 Where the interaction ameliorates a fitness limiting stress in both species, mutations in one
122 species that reduce stress on a partner species can simultaneously increase fitness in both species.
123 The increase in fitness of the partner species increases the frequency or extent of the interaction
124 for the first species, ameliorating more stress and positively impacting fitness. This phenomenon
125 is known as fitness feedback (Sachs et al., 2004), and such mutations will be favored by selection.
126 Genetic variation in the traits of one partner that ameliorate stress in the other should thus impact
127 fitness of both partners in these stressful sites. As selection continues to fix mutations amelio-
128 rating the stress of partners, we predict increasing mutual benefit at stressful or resource-limited
129 ends of environmental gradients due to fixation of mutations in both partners (mutualistic co-

130 adaptation) or just one partner alone (mutualistic adaptation, Figure 1).

131 At the ends of gradients that are “benign” with respect to stresses or resources, fitness will
132 be instead limited by either costs of the interaction or by unrelated factors. Interactions between
133 species may become neutral or shift towards antagonism (Johnson, 1993; Bertness and Callaway,
134 1994; Schwartz and Hoeksema, 1998), which we predict will result in a variety of coevolutionary
135 outcomes.

136 If the interaction is neutral for one or more partners, we predict no co-adaptation, though if
137 the interaction continues to negatively or positively impact fitness of one partner, adaptation in
138 this partner will still be influenced by the interaction. For example, in shifts of plant-plant compe-
139 tition towards facilitation with increasing stress, facilitation is often not mutual (He et al., 2013;
140 Schöb et al., 2014*b,a*). When interactions do not alter fitness, mutations that increase investment
141 in interactions will drift, or will be removed by selection if the investment itself is costly to pro-
142 duce.

143 When the interaction is antagonistic in benign conditions (-,- or +,-), the interaction may
144 again strongly affect fitness, now inflicting high costs on one or both partners (Figure 1). Re-
145 ciprocal selection in mutually antagonistic interactions (-,- as in many competitive interactions)
146 could act either to reduce antagonistic interactions through avoidance of the interaction entirely
147 (such as character displacement, Pfennig and Pfennig, 2009), or to avoid fitness costs through
148 tolerance (Bronstein, 2009). Both of these responses to antagonistic interactions reduce the ef-
149 fects of the interaction on fitness, and reduce the strength of selection imposed by each species.
150 Asymmetric antagonisms (+,-), such as trophic interactions (e.g. parasitism, predation), can re-
151 sult in asynchronous or oscillating Red-Queen coevolutionary dynamics such as arms-races (Toju
152 et al., 2011) or frequency-dependent selection (Decaestecker et al., 2007). In particular for arms-
153 races, this intensified coevolution in benign conditions will escalate offensive and defensive traits
154 to more extreme values (Hochberg and van Baalen, 1998; Benkman et al., 2003; Hanifin et al.,
155 2008). Mutations affecting asymmetric interaction outcomes will have high fitness consequences
156 and will either swiftly fix or could exhibit cyclical dynamics under frequency-dependent selec-

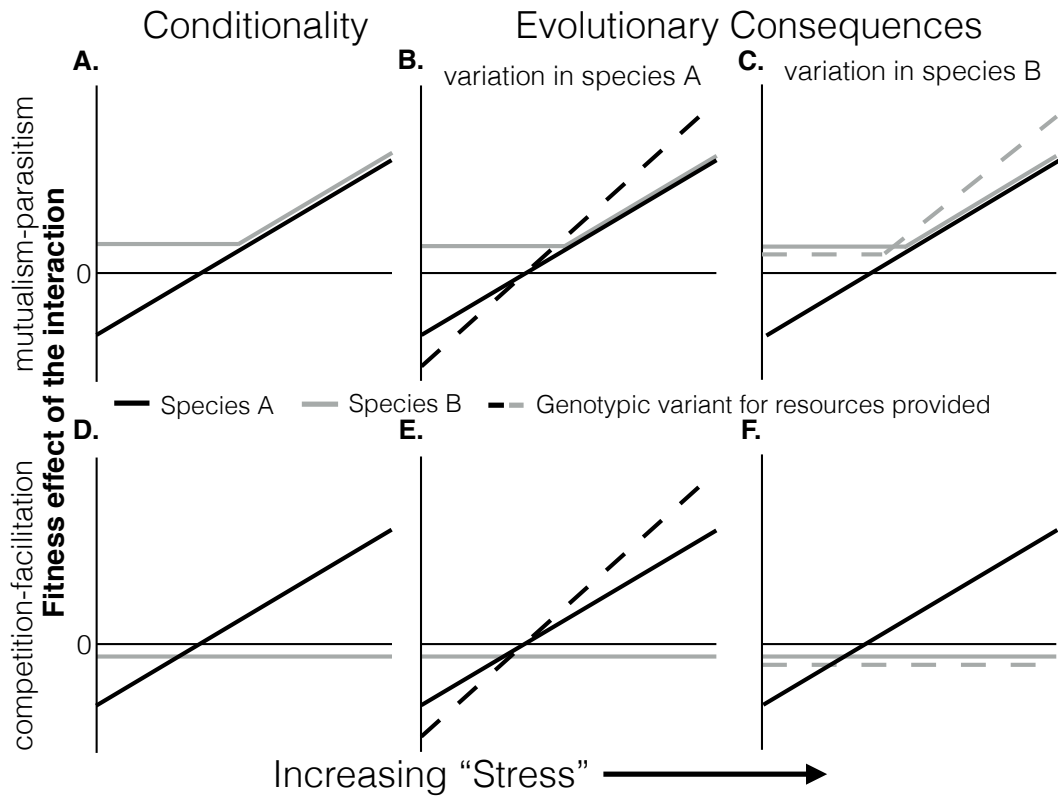


Figure 1: Conditionality hypotheses (A,D) and CoCoA predictions (B,C,E,F) at low and high stress. A-C, from parasitism to mutualism; D-F, from competition to facilitation. A & D, interaction outcomes shift towards more positive interaction outcomes at more stress-limited sites, as predicted by generalizing either SGH or limiting resource conditionality. B, E, the fitness of a variant of species A (the species parasitized at low stress in B and facilitated in E) that provides more benefit to species B (the species parasitic at low stress in B and the facilitator in E) across interaction types and shifts is now depicted next to the original genotype in dashed line. C,F, the same, but for variation in species B. Depending on the interaction type and stress, the selection on species A and B would favor the variant, original genotype, or neither, but variants are more favored (or less disfavored) at higher stress. CoCoA thus suggests increasing mutualistic local co-adaptation or adaptation at high stress sites, and where interactions grade into increasing antagonism (+,- or -,-), increasing antagonistic co-adaptation (for +,-) or adaptation to avoid interactions (for -,-) is favored.

157 tion.

158 Evidence exists that many traits affecting interaction outcomes have a genetic basis and can
159 respond to selection. For example, variation in mutualistic benefit provided has been shown to
160 have a genetic basis in many systems (e.g. Moran, 2001; Eaton et al., 2015; Klinger et al., 2016;
161 Batstone et al., 2017) as has variation in resistance to antagonists (e.g. Staskawicz et al., 1995;
162 Lively and Dybdahl, 2000; Decaestecker et al., 2007), and thus both can be expected to respond
163 to selection.

164 Both theoretical and empirical work suggest that as the strength of selection on beneficial or
165 antagonistic interactions increases, mutations improving interaction outcomes with local part-
166 ners are more likely to fix (Parker, 1999; Nuismer et al., 2000; Kawecki and Ebert, 2004; Thomp-
167 son, 2005; Schemske et al., 2009). Strong selection coupled with low gene flow is predicted to
168 result in specific adaptation or co-adaptation between local populations. While extremely high
169 gene flow would prevent adaptation along any gradient, intermediate gene flow could preclude
170 local adaptation/co-adaptation within populations and instead promote general adaptation/co-
171 adaptation among sets of populations. We define specific benefit mutations as those that are spe-
172 cific to the genotypes of local partners (“specific benefits”). Specific-benefit mutations should fix
173 under low gene flow while mutations underlying benefits to and from multiple partners (“gener-
174 alized benefits”) are predicted to be favored when gene flow between stressful sites is higher (see
175 also, “Interpretation of Results”, Figure 2).

176 In sum, we predict that interactions with net fitness effects that shift in sign or strength along
177 gradients will generate the most adaptation or co-adaptation near gradient extremes and least
178 midrange, where neutral or reduced fitness impacts on one or more species prevent feedbacks.
179 We predict evolution towards increasing mutualism and/or greater mutualistic co-adaptation
180 where the interaction most ameliorates fitness-limiting stress. In contrast, we predict antagonistic
181 evolutionary dynamics at benign sites, where interaction outcomes are expected to be more an-
182 tagonistic. We call this the **(Co)-adaptation to Conditionality across Abiotic gradients hypothesis**,
183 or **CoCoA**.

184 Below, we discuss designs that can test CoCoA. In designing a test for CoCoA, we focus pri-
185 marily on interactions that are mutualistic either along part or the full length of the stress gradi-
186 ent, as we predict the coevolutionary outcomes will be consistent over time in mutualistic zones
187 of the gradient, making these populations most straightforward to test at a single timepoint. In
188 contrast, antagonistic coevolution is predicted in more benign conditions. It is well-known that
189 antagonistic coevolution is difficult to test, as many patterns are consistent with, but not indicative
190 of, antagonistic coevolution (see e.g. Lively and Dybdahl, 2000; Nuismer et al., 2000; Nuismer,
191 2006; Gandon et al., 2008; Frederickson, 2013; Stuart and Losos, 2013).

192 **Testing for CoCoA**

193 Tests of CoCoA should include: (1) evidence of an environmental gradient that ranges from lim-
194 iting to non-limiting for one (only adaptation predictions for the limited species are relevant) or
195 both (all CoCoA predictions) partners; (2) evidence that the net fitness impact of the interaction
196 on partners changes across the gradient due to changes in stress limitation; (3) measures of fitness
197 outcomes in interactions with local and non-local partner pairs sourced from populations across
198 the gradient. Throughout, we refer to populations of each species from the same site as sympatric
199 and populations from different sites as allopatric. Measurements of partner effects on fitness must
200 include both sympatric and allopatric partners to test for both generalized and specific benefits.
201 Specific benefits (see above) could arise from specific populations of both species co-adapting to
202 the other (specific co-adaptation), or only one species population adapting to the other if the inter-
203 action is $+0$ (specific adaptation). Generalized benefits would arise if heritable traits adaptively
204 increased the benefits provided to any partner (i.e. across multiple populations) at stressful sites
205 (generalized adaptation or co-adaptation). Below we outline experimental designs and models to
206 test CoCoA, and discuss interpretations of results.

207 **Experimental design**

208 The ideal test of CoCoA will quantify two things. First, it will quantify the effects of the inter-
209 action on the fitness of both species sampled from across the gradient. Despite widespread doc-
210 umentation of conditionality (Chamberlain et al., 2014), abiotic predictors of conditionality re-
211 main unclear for many species interactions (for example, Maron et al., 2014). Second, the ideal
212 test will quantify the extent of generalized and specific benefits between partner species across
213 the gradient. For illustration, we provide an example test for the interaction between two species
214 (Species “A” and “B”) along a gradient from stressful conditions, where CoCoA and condition-
215 ity hypotheses predict that species will mutually enhance each others’ fitness, to conditions where
216 at least one species is predicted to have a negative effect on the other. CoCoA applies to other
217 interactions that may span different outcome ranges across limiting stresses (e.g. competitive in
218 benign sites to commensal in stressful sites), which can be tested in the same fashion. Except for
219 interactions that never become commensal or mutually positive, the single timepoint tests are suf-
220 ficient.

221 Testing CoCoA requires sampling populations of both species at sites along an identified
222 stress gradient using the general approach proposed by Blanquart et al. (2013). To this approach,
223 we add sources of populations across a gradient, and inclusion of gradient effects on fitness out-
224 comes in the analyses. More populations always improves power, since population source site
225 is the experimental unit, yet the number of populations must be balanced with the replication
226 needed for each comparison. Under CoCoA, we predict increased generalized and specific ben-
227 efits accruing from adaptation of partners at the stressful end of the gradient. In order to test for
228 generalized adaptation (Figure 2, B and D, solid lines), one can regress the effect of Species B
229 source population on Species A fitness across all populations of Species A sampled along the gra-
230 dient. For example, a significant positive global effect on Species A fitness from interacting with
231 a single population of Species B indicates that selection has favored generalized mutualistic traits
232 in that Species B population. To quantify specific adaptation or co-adaptation between local pop-
233 ulations of partners, it is necessary to assess the relative benefits received by both Species A and

234 Species B with sympatric partners versus allopatric partners across the gradient (Figure 2, C and
235 D, difference between dashed and solid lines).

236 While these comparisons may be made using all possible combinations of interacting partner
237 populations of Species A and B, a fully crossed design is not required. We suggest designs that
238 have twice as many allopatric as sympatric comparisons across the gradient. Power to estimate
239 local adaptation in sympatry is maximized when the number of allopatric and sympatric com-
240 parisons are equal, and with the largest feasible number of populations (Blanquart et al., 2013).
241 However, because our model includes a formal gradient term, and interactions with that gradient,
242 our design requires additional allopatric comparisons relative to the number of sympatric com-
243 parisons. Paired populations of both Species A and B must be sampled from the same sites, and
244 should be sampled to span the gradient, including intermediate sites, as stress is modeled as a
245 continuous gradient in our approach. Sampling of paired populations across the gradient allows
246 allopatric comparisons for each population from a source site of similar stress level, which in-
247 creases the power to estimate change in sympatric effect across source site stress.

248 Random experimental combination of sampled populations will increase several biases in es-
249 timating allopatric effects. Populations sourced from the lowest stress sites will be more often
250 combined with partners from sites with higher stress (intermediate and high) than other low stress
251 sites (and vice versa). Populations from the highest and lowest stress sites will have a larger
252 range in the difference in stress between their own source site and comparison population sites.
253 A variety of designs minimize potential biases, and we provide one example in Figure 3.

254 Experiments should be run under conditions representative of those observed in natural pop-
255 ulations, as inappropriate conditions may alter expressed benefits or costs of associating with
256 partners (Lau and Lennon, 2012). Ideally, fitness measures will be as close to absolute fitness as
257 possible, such as number of viable offspring. Running the experiment in multiple common gar-
258 dens with different conditions allows a test of the CoCoA prerequisite that increasing stress shifts
259 interaction outcomes towards increasing mutualism at high stress. While repeating in multiple
260 environments is optimal, it may be possible only in systems where massive replication is feasi-

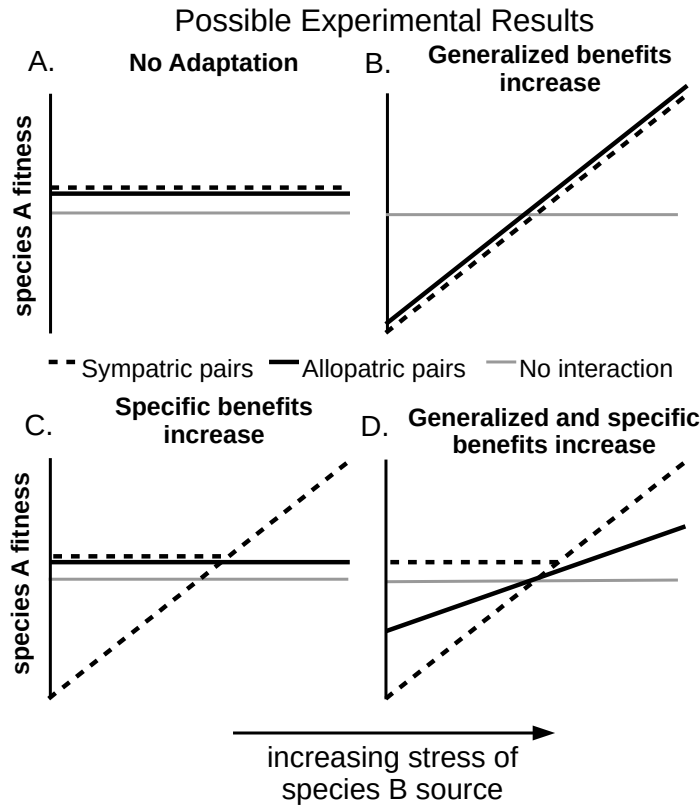


Figure 2: Possible experimental outcomes under high stress conditions. CoCoA predicts greater generalized fitness benefits provided by partners sourced from stressful sites across allopatric (solid lines) and sympatric (dashed lines) combinations (B, D). CoCoA predicts increasing specific fitness benefits of sympatric combinations with source stress (increasing difference of dashed and solid lines, C, D). For combinations with partners from benign sites, CoCoA predicts variable outcomes (multiple dashed lines), and no (A,C,D) or negative (B-D) sympatric effects. Increasing costs of sympatric partners as environments become more benign would indicate antagonistic adaptation, but might only be observed for one species, and other possibilities exist (see text). With antagonistic co-adaptation, a more likely result is high variance among population sympatric effects, if population pairs are at different stages in Red-queen dynamics. However, high variance in sympatric effects could alternately result from drift, and so is not a useful test. Without co-adaptation or adaptation, CoCoA expects no sympatric effects or difference across gradients (A). As a reference point, species A fitness without interacting with species B is shown in grey.

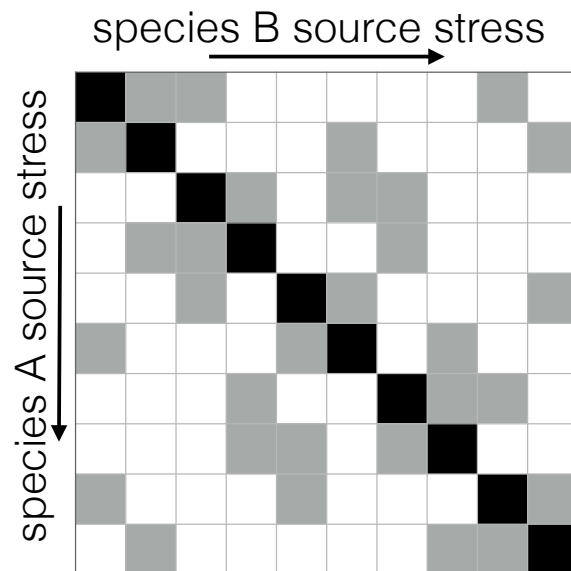


Figure 3: Possible sampling design and experimental combinations. Species A sources are in rows, arranged by increasing stress of source site from top to bottom. Species B sources are in columns, arranged by increasing stress of source site from left to right. Filled in squares are experimentally paired populations of A and B, including twice as many allopatric (grey) as sympatric (black) comparisons, and spreading sympatric and allopatric comparisons along the stress gradient for sources of both species A and species B.

261 ble, such as in microbe-microbe interactions. Field environments have the benefit of being a more
262 realistic context in which to test for co-adaptation between local populations, but are often con-
263 strained in replication both for the number population sources and the number of common garden
264 (sensu lato) sites. We propose that a minimal design tests outcomes under conditions represent-
265 ing the stressful end of the gradient, which should maximize detection of mutualistic adaptation
266 or co-adaptation. Here, our experimental design and analysis tests CoCoA predictions for this
267 stressful region of the gradient (e.g., under reduced resources, water availability, etc.).

268 **A linear model framework**

269 In classic tests of local adaptation, populations and sites are treated as discrete entities (Kawecki
270 and Ebert, 2004; Blanquart et al., 2013). Our approach to detect local adaptation along a gradient
271 uses a continuous approach to analyze gradient effects. We suggest modeling effects of partners
272 and environments on fitness in a linear framework (non-linearity discussed below), where fitness
273 in one focal partner at a time is the response variable Y (below), and then repeating across the
274 other partner so that species A and B fitnesses are response variables in separate models. This
275 linear testing framework defines generally better and worse mutualists using average fitness ben-
276 efits conferred to partners across partner combinations, which follows recent advances in theory
277 (Frederickson, 2013; Jones et al., 2015). Below we show Species A fitness as the response (Y_A);
278 the model for Species B fitness would be specified by swapping all A and B terms.

$$Y_A \sim \alpha + \beta_{E_B} E_B + \beta_S S + \beta_{E \times S} E \times S + \beta_{E_A} E_A + \beta_Z Z + \varepsilon$$

279 The estimated parameter for the main effect of source environment of the non-focal partner
280 (here, the environment of Species B population source, E_B , parameter β_{E_B}) is a test of the CoCoA
281 prediction that Species B sourced from more stressful sites might be generally more mutualistic
282 for all Species A populations than Species B sourced from the less stressful parts of the gradient.
283 CoCoA predicts that β_{E_B} should be positive.

284 Models include a slope parameter for the binary term (S) indicating whether origins of the

285 interactors are sympatric ($S = 1$) or allopatric ($S = 0$) in addition to the slope parameter for the in-
286 teraction between sympatry and the environmental gradient of source ($\beta_{E \times S}$), because we predict
287 sympatry effects to vary across the gradient. Parameter estimates for effects of non-focal partner
288 source environments (β_{E_B}) compared to estimates for the environment interaction with sympa-
289 try (an environment \times sympatry interaction denoted as $E \times S$) allow us to tease apart generalized
290 benefits from specific benefits along the gradient (Figures 2 & 4). CoCoA predicts that without
291 extensive gene flow between high stress sites, $\beta_{E \times S}$ should be positive; specifically that bene-
292 fits accrued by sympatric partners from most stressful sites should be relatively greater than the
293 benefits accrued by sympatric partners from other parts of the gradient, e.g. specific benefits are
294 increased for stressful sites.

295 The focal partner source environment (here, the environment E_A) is included to account for
296 any main effects of population fitness along the gradient, as selection to reduce the fitness-limiting
297 stress may not act only on interactions. For example, selection may increase tolerance of stress
298 without interactions (Espeland and Rice, 2007), or low resource environments might select for
299 smaller individuals than high resource environments. If such effects are large, they can cause
300 over- or under-estimation sympatric effects (Blanquart et al., 2013). Since the slope of species
301 A fitness along increasing source site stress of B partners is built from the sum of β_{E_A} , β_{E_B} , and
302 $\beta_{E \times S}$ (Figure 4), failure to account for β_{E_A} can affect estimates of $\beta_{E \times S}$ if fitness of Species A is
303 positively or negatively correlated with the stress gradient. Estimating β_{E_A} allows us to account
304 for either of these other sources of correlation (see Blanquart et al., 2013).

305 Our above model assumes, and our figures (1,2,4) depict, a linear relationship between fit-
306 ness and the environmental gradient. To assess whether non-linear effects of gradients are better
307 descriptors of the effects on fitness of species interactions along gradients (e.g. Malkinson and
308 Tielbörger, 2010; Holmgren and Scheffer, 2010), and subsequent adaptation patterns, models
309 with quadratic terms for E_B and $E \times S$ should be compared with models using linear terms. Var-
310 ious types of non-linearity may be relevant, such as threshold or parabolic models, especially for
311 interactions where peak mutualism or facilitation might be at mid-stress (see “Other considera-

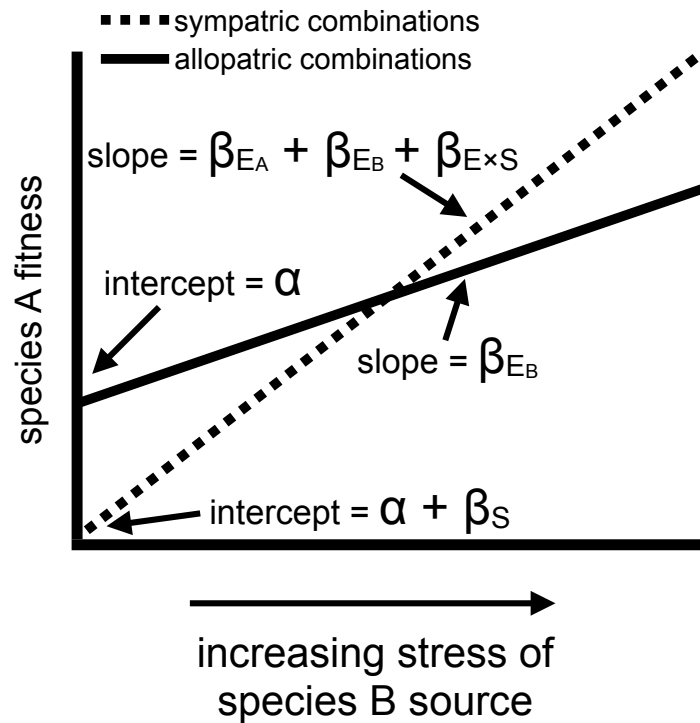


Figure 4: Here we relate model parameters to linear relationships between fitness and partner source, drawn here for the scenario in Figure 2 D. Generalized coevolutionary benefits are tested by the parameter β_{E_B} , the slope of the allopatric comparisons (solid line). Specific coevolutionary benefits are tested by the parameter $\beta_{E \times S}$, which, when added to β_{E_B} and β_{E_A} , is the slope of the sympatric (dashed) line. β_S only affects the intercept of the sympatric line. $\beta_{E \times S}$ alone describes the increasingly positive difference between allopatric and sympatric combinations as the source site becomes more stressful.

312 tions” below). Additional random effects that might be required, depending on the design, could
313 include: family effects, block effects, or year effects (represented here as a generic Z , with pa-
314 rameter β_Z).

315 **Interpretation of results**

316 The predictions of CoCoA would be supported by the following outcomes: 1) if partners from
317 more stressful sites provide greater benefits across all focal species populations than partners
318 from less limiting sites (generalized benefits, β_{E_B} significantly positive) and 2) if benefits that
319 are provided to sympatric partners over allopatric partners are greater for populations from stress-
320 ful sites (greater specific benefits, indicated by a significant and positive $\beta_{E \times S}$). When both β_{E_B}
321 and $\beta_{E \times S}$ are significant and positive, both predictions of CoCoA are supported, and both al-
322 lopatric and sympatric lines will have a positive slope (see Figure 4), but the sympatric line will
323 be steeper (illustrated in Figure 2 D). For interactions that grade into facilitative commensalism
324 (not depicted in Figures 2 and 4), we still expect to see increasing generalized and/or specific
325 benefits, as for interactions that grade into mutualisms. However, such patterns should only be
326 detected for the facilitated species.

327 Extensive gene flow between populations at stressful sites could result in more mutualistic
328 partners from highly limited sites without increased local adaptation. For example, populations
329 might experience isolation by environment more than isolation by distance (e.g. Sexton et al.,
330 2016). This scenario would be indicated by the case that $\beta_{E \times S}$ is non-significant and β_{E_B} is sig-
331 nificant and positive. The slope of the allopatric and sympatric lines would be identical (Figure
332 2B), or differences would be due only to patterns in fitness of the focal species across the gradi-
333 ent, β_{E_A} , unrelated to species interactions.

334 This section has focused on the stressful ends of gradients and interactions that at least grade
335 into mutualistic (+,+) or commensal (+,0) outcomes. A similar experimental design and model
336 would be required for tests of CoCoA in antagonisms or at benign ends of the gradients. β_S tests
337 the main effect of sympatry, and is the intercept adjustment of the sympatric line relative to the

338 non-sympatric line (Figure 4). This term reflects the difference between allopatric and sympatric
339 pairings of A and B from benign sites. When this parameter is negative (as in Figure 2, B and
340 D), it would indicate antagonistic adaptation in the non-focal species in benign sites. However,
341 an estimate of β_S that is positive or not different from 0 does not necessarily indicate a lack of
342 antagonistic adaptation or co-adaptation, as adaptation in antagonistic interactions can gener-
343 ate non-significant effects (due to e.g. temporal or spatial variation in adaptation cycles, see be-
344 low). Experimental evolution, especially with the ability to archive and resuscitate genotypes (in
345 species with resting propagules), would allow detection of whether local mutualistic adaptation
346 proceeds reciprocally (co-adaptation) or if one species alone produces all patterns of adaptation.
347 CoCoA expects the same patterns in increasing specific benefits with stress regardless of whether
348 responses to selection are reciprocal (local co-adaptation) or restricted to one species (adaptation
349 only); benefits measured in sympatric pairs do not separate contributions of adaptation in each
350 species.

351 **Other considerations**

352 A non-trivial matter is how the gradient is defined and identified. Specifically, for CoCoA to
353 hold, not only must sites be stressful, but interactions between partners must ameliorate the stress.
354 CoCoA will be predictive when conditions for the SGH and limiting resource conditionality are
355 met: when a stress ranges from non-limiting to strongly limiting of fitness and is ameliorated by
356 interaction between the focal species (He and Bertness, 2014). CoCoA will further be most pre-
357 dictive when gene flow is sufficiently restricted to allow local adaptation and there is genetic vari-
358 ation on which selection can act in both partners. CoCoA will be less informative across weak,
359 non-limiting, or multiple co-occurring gradients, where importance of interactions to fitness is
360 less predictable (He and Bertness, 2014).

361 While extensive research on the SGH in plant-plant interactions generally supports the pre-
362 diction of increasing facilitation with stress (He et al., 2013), peak facilitation may occur in sites
363 with moderately, rather than extremely limiting stress (Michalet et al., 2006; Holmgren and Schef-

364 fer, 2010; Malkinson and Tielbörger, 2010). Such intermediate peaks could be generated by non-
365 linear relationships between benefits (or costs) and abiotic gradients (Holmgren and Scheffer,
366 2010), or by low density of individuals at high stress sites causing missed interactions (Travis
367 et al., 2006). Intermediate peaks appear to fit best in interactions that grade from increasing to
368 decreasing access to a shared limiting resource (Maestre et al., 2009; Michalet et al., 2014), as
369 opposed to interactions with differing limiting resources between partners. Plant-pollinator bene-
370 fits also can show intermediate peaks, because relationship between pollination limitation and fit-
371 ness limitation often changes non-linearly across environments (Haig and Westoby, 1988; Maron
372 et al., 2014). Non-linearity also makes sense in light of the fact that there may be little interac-
373 tions can do in the face of extreme stress, and if they no longer ameliorate the stress, then selec-
374 tion will no longer favor investment in the interaction. Peaks for positive outcomes in moderately
375 stressful conditions, regardless of mechanism, have the consequence for CoCoA that mutualistic
376 adaptation and co-adaptation would also peak at moderately stressful conditions, in which case,
377 non-linear models for fitness across stress gradients would be needed (see “A linear model frame-
378 work” above).

379 Source site differences along the stress gradient may affect fitnesses of partner pairings. In
380 studies of climate adaptation, functions of environmental distance transfer from source site to
381 experimental site better predict success than experimental site environment alone (Wang et al.,
382 2010). If species interactions have analogous dynamics, instead of or in addition to CoCoA, then
383 such transfer functions between source sites of experimental combinations would determine their
384 ability to mutually benefit from each other, rather than dynamics of local and mutualistic adapta-
385 tion. For example, we combine CoCoA effects with the transfer function of Wang et al. (2010),
386 by adding squared source environment terms and an interactive slope, $\beta_{E_A \times E_B}$:

$$Y_A = \alpha + \beta_{E_B} E_B + \beta_{E_B} E_B^2 + \beta_{E_A} E_A + \beta_{E_A} E_A^2 + \beta_{E_A \times E_B} E_A \times E_B + \beta_S S + \beta_{E \times S} E \times S + \varepsilon$$

387 The quadratic model of Wang et al. (2010) here now implies that there is either an optimal
388 environmental distance (i.e. potentially 0 for mutualisms), or least optimal distance between
389 sources of partner populations along the environmental gradients. As the distance between pop-
390 ulation pairs increases, fitness effects on the focal species either increase or decrease, depending
391 on parabola sign. As before, the addition of sympatry, and sympatry-by-environment effects just
392 add the local (co)-adaptation effects we have discussed here, and generalized benefits are cap-
393 tured by the linear source environment terms. Power to estimate such transfer functions, would be
394 improved by many more population comparisons than demonstrated in Figure 3 (see Wang et al.,
395 2010).

396 We have focused our tests and predictions around conditions that predict mutualistic coevo-
397 lution (high stress) because coevolutionary patterns from antagonisms (predicted in benign con-
398 ditions) are more difficult to detect. Character displacement in $-,-$ interactions is notoriously dif-
399 ficult to document (Stuart and Losos, 2013). Similarly, in $+,-$ interactions, one species may be
400 “winning” the battle and appear locally adapted at a single timepoint, but the winning species
401 is likely to vary across both timepoints and space as evolution in the other species counteracts
402 “gains” (e.g. Van Valen, 1974; Gandon and Michalakis, 2002; Nuismer, 2006). Running this
403 experiment multiple times from populations collected at different timepoints (see Decaestecker
404 et al., 2007), or across experimental evolution (see Pascua et al., 2011) would allow differentia-
405 tion between drifting variation in sympatric effects and Red Queen dynamics. Long-term sam-
406 pling of trait changes and genotypes (Dybdahl and Lively, 1998; Decaestecker et al., 2007), as
407 well as long term partner removal experiments (Stuart and Losos, 2013), have also proven to be
408 effective tools for detecting antagonistic coevolution, and would be equally useful for testing Co-
409 CoA predictions in antagonistic interactions. Regardless of the test, conclusions must be based on
410 degree of trait change or rate of evolutionary dynamics across both abiotic gradients and time.

411 **Existing literature pertinent to CoCoA**

412 In reviewing the literature, we found a number of studies in which most, but not all, of the criteria
413 required to evaluate CoCoA have been tested, but only one study that has addressed all criteria.

414 These studies, however, have some evidence related to the predictions of CoCoA.

415 Experimentation on plant-microbe interactions offer the most complete tests. The outcomes
416 of interactions between plants and rhizosphere biota (a diverse community of microbes living in
417 and near roots Hiltner (1904)) are highly influenced by environments (e.g. Zhu et al., 2009; Smith
418 and Read, 2008; Lau and Lennon, 2012). Limiting soil nutrients have frequently been identified
419 as the potential driver of the evolution of interactions with soil rhizosphere microbes (Johnson,
420 1993; Schwartz and Hoeksema, 1998; Kiers and van der Heijden, 2006; Bever, 2015), and meta-
421 analysis finds local adaptation in plants and mycorrhizal fungi to be common but not universal
422 (Rúa et al., 2016).

423 Johnson et al. (2010), which met all of the above criteria, found mutualistic local adaptation
424 between a grass and its associated arbuscular mycorrhizal fungi across a phosphorus gradient.
425 Plants are generally known to derive increased benefits from interacting with these fungi in low
426 phosphorus conditions (Smith and Read, 2008). Fungi sourced from low phosphorous sites were
427 more beneficial across plants but provided even greater benefits to sympatric plants (Johnson
428 et al., 2010), supporting both the specialized and generalized benefits predictions of CoCoA.
429 However, as only three sites were sampled, we remain cautious of inferring strong support for
430 CoCoA. Other studies sample outcomes along environmental stress gradients, but do not explic-
431 itly include sympatric and allopatric partners to evaluate the nature of benefits or local adapta-
432 tion (specific or generalized). Barrett et al. (2012) cross-inoculated acacias and microbes sam-
433 pled along a soil nitrogen gradient (likely a limiting stress gradient), and found that the effects of
434 soil microbes sampled from low nitrogen sites provided the greatest benefit to acacias. In a study
435 of plants and nitrogen-fixing bacteria, bacterial genotypes sampled from high nitrogen sites (in
436 which nitrogen is less limiting to plants) similarly provided less benefits than genotypes from low
437 nitrogen sites (Weese et al., 2015).

438 In many ant-plant mutualisms, ants protect plants from herbivory and receive food from the
439 plant. In drier sites, plants are limited by both water and herbivory costs, and ants are likely lim-
440 ited by plant-fixed carbon (Pringle et al., 2013). In such dry, limited sites, ants invest more in
441 plant defense, reducing herbivory limitation, and plants allocate more carbon to ants, increas-
442 ing ant colony size (Pringle et al., 2013). In Pringle et al. (2013), lower water sites were limiting
443 for a plant host because insufficient water increased the risk of plant death from herbivory. This
444 example documents both the limiting gradient, which is ameliorated by the interaction for both
445 partners, and greater reciprocal mutualistic benefits at the stressful portion of the gradient. It re-
446 mains to be seen whether these benefits are adaptive differences or plastic behaviors, and whether
447 they are generalized or specific.

448 Plant-plant interactions across mesic-arid gradients range in outcome from antagonistic to
449 facilitative as aridity increases (He et al., 2013), leading to the prediction of CoCoA that adapta-
450 tion to competitors would be greatest in mesic sites and adaptation of beneficiaries to facilitators
451 greatest in arid sites. Existing evidence does not reject CoCoA, but also does not offer complete
452 tests: genotypes of plants from mesic (benign) sources were least affected by competition in mul-
453 tiple systems (Liancourt and Tielbörger, 2009; Liancourt et al., 2013), and another study found
454 greater evidence for plant local adaptation in mesic sites when neighbors are included (Ariza and
455 Tielbörger, 2011). However, a test of adaptation in plant-plant interactions from a different stress
456 gradient (soil chemical stress) suggests that adaptive increases in stress-tolerance may be more
457 important than adaptive increase in benefit from facilitation (Espeland and Rice, 2007).

458 Bacteria-phage systems at the conditions least stressful for bacteria (high nutrients) show
459 strongest local adaptation (receipt of specific benefits) of phages to host bacteria (Pascua et al.,
460 2011). Pascua et al. (2011) also showed increasing overall infectivity and resistance in high nu-
461 trient conditions, suggesting greater trait escalation. Another study found the reciprocal expecta-
462 tion: less stressful conditions for bacteria led to evolution of increased defense traits in bacteria
463 when phages and bacteria were permitted to evolve (Zhang and Buckling, 2016).

464 Increased trait escalation at high productivity (indicating low plant stress) has also been found

465 in camellia-weevil antagonisms, where camellia defensive and weevil offensive (Toju et al., 2011)
466 traits appear to have escalated more. However, it is clear that not all plant-herbivore interactions
467 change in outcome the same way across plant productivity gradients (Maron et al., 2014). In sites
468 where prey are physiologically less limited, defensive traits appear to have escalated more in
469 newt-predator (Stokes et al., 2015) and squirrel-rattlesnake (Holding et al., 2016) predator-prey
470 antagonisms. These systems show some of the patterns CoCoA would predict, but whether stress-
471 gradients led to these patterns, or whether patterns reflect adaptation to interactions must still be
472 tested.

473 In contrast, we found only one study with evidence in conflict with CoCoA predictions. Across
474 a gradient of increasingly cold conditions, plants show no local adaptation with rhizosphere biota
475 and no evidence of increasing benefits from colder sourced biota (Kardol et al., 2014). While the
476 extreme cold is very likely to be stressful, and the ability of interactions plant-rhizosphere biota
477 to reciprocally ameliorate effects of extreme cold also likely (Zhu et al., 2009), they were not
478 tested.

479 In sum, while current evidence offers mixed support, only very few tests of CoCoA exist.
480 Complete tests of CoCoA are within reach in many more systems, and evidence above suggests
481 that complete tests of CoCoA as outlined above would be worthwhile.

482 **Discussion**

483 Economic and stress-gradient models of conditionality in species interactions predict shifts in
484 species interactions from more negative outcomes to more positive outcomes as environmental
485 stress (Bertness and Callaway, 1994; Brooker and Callaghan, 1998; Malkinson and Tielbörger,
486 2010) or resource limitation (Johnson, 1993; Schwartz and Hoeksema, 1998) increases (see Fig-
487 ure 1).

488 We present here an extended hypothesis for the evolutionary consequences of these models
489 of ecological conditionality, which we term Co-adaptation to Conditionality across Abiotic gra-
490 dients (CoCoA). CoCoA predicts increasingly strong (co-)evolutionary dynamics where con-

ditionality models predict increasingly positive or increasingly negative interaction outcomes. At stressful sites where partners mutually enhance each others' fitness, or one partner receives increasing benefits, mutualistic co-adaptation and adaptation are predicted to dominate, respectively. In benign sites where the interaction shifts towards parasitic, or mutually negative, CoCoA predicts intensification of evolutionary dynamics: Red Queen (or similar) coevolutionary scenarios for parasitic outcomes, and adaptation to avoid interactions such as character displacement (Pfennig and Pfennig, 2009) or habitat partitioning (Martin, 1998), for mutually negative outcomes. Between these extremes, in intermediate stress or benign environments, interaction outcomes approach neutrality, leading to predictable zones of no adaptation.

Other models of co-adaptation (Johnson, 1993; Schwartz and Hoeksema, 1998; Thrall et al., 2007; Bever, 2015) and behavioral models (Revillini et al., 2016), focus on environmental gradients. Like CoCoA, some models (Johnson, 1993; Schwartz and Hoeksema, 1998; Bever, 2015) predict that selection in resource-limiting environments should favor increased benefits provided to partners in the mutualism. Alternatively, Thrall et al. (2007) make predictions based on levels of environmental productivity and biological diversity. CoCoA differs from these models in its focus on adaptation patterns in both partners, its inclusion of fitness-limiting stresses beyond resources, and thus its applicability to a wide variety of conditional interactions.

CoCoA implies that selection for specialization may be common at both ends of the stress gradient continuum, i.e. in both antagonistic and mutualistic interactions. While it is generally accepted that parasitism often promotes specialization and increases the rate of evolution (Pater-son et al., 2010), it is debated whether mutualism commonly imposes selection for specialization (Thompson, 2005). There is, however, some evidence that mutualism can be at least as strong a driver for specialization as parasitism (Kawakita et al., 2010), and mutualists may evolve at equal or faster rates than non-mutualist sister lineages (Rubin and Moreau, 2016).

515 **Concluding Remarks**

516 As climatic conditions become more extreme and stressful under global change (Pachauri et al.,
517 2014), we predict that adaptation to changing environments may be heavily influenced by biotic
518 interactions. Numerous studies have focused on single species processes that limit ranges, such
519 as source-sink dynamics or maladaptive gene flow (see Sexton et al., 2009, for review), but our
520 CoCoA hypothesis suggests more research on multi-species dynamics may be fruitful (Sexton
521 et al., 2009; van der Putten et al., 2010).

522 CoCoA contributes to a growing body of literature highlighting the importance of biotic inter-
523 actions in determining limits of species distributions across abiotic gradients (e.g. HilleRisLam-
524 bers et al., 2013; Afkhami et al., 2014), even in climatically stressful environments (e.g. Brown
525 and Vellend, 2014) where abiotic variables have often been thought to be of greater importance
526 (Brown et al., 1996; Hargreaves et al., 2014). Biotic filters on abiotic variables that exacerbate
527 or ameliorate abiotic effects may thus have widespread consequences for range shifts and other
528 responses to global change.

529 **Acknowledgements**

530 AO was supported by NSF GRFP grant DGE-1148897 and NSF grant DEB-0919559 to SYS.
531 J.R.I. would like to thank support from NSF Plant Genome (project IOS-1238014) and USDA
532 (Hatch project CA-D-PLS-2066-H). R.J.H.S would like to thank support from CONACYT (CB15-
533 25401). The authors would like to thank the Coop, Schmitt, Strauss, and Ross-Ibarra labs at UC
534 Davis for discussion.

535 **References**

- 536 Afkhami, M. E., P. J. McIntyre, and S. Y. Strauss. 2014. Mutualist-mediated effects on species'
537 range limits across large geographic scales. *Ecology Letters*, 17:1265–1273.
- 538 Ariza, C. and K. Tielbörger. 2011. An evolutionary approach to studying the relative importance
539 of plant-plant interactions along environmental gradients. *Functional Ecology*, 25:932–942.

- 540 Barrett, L. G., L. M. Broadhurst, and P. H. Thrall. 2012. Geographic adaptation in plant–soil
541 mutualisms: tests using acacia spp. and rhizobial bacteria. *Functional Ecology*, 26:457–468.
- 542 Batstone, R. T., E. M. Dutton, D. Wang, M. Yang, and M. E. Frederickson. 2017. The evolu-
543 tion of symbiont preference traits in the model legume *medicago truncatula*. *New Phytologist*,
544 213:1850–1861.
- 545 Benkman, C. W., T. L. Parchman, A. Favis, and A. M. Siepielski. 2003. Reciprocal selection
546 causes a coevolutionary arms race between crossbills and lodgepole pine. *The American Natu-
547 ralist*, 162:182–194.
- 548 Bertness, M. D. and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology
549 & Evolution*, 9:191–193.
- 550 Bever, J. D.. 2015. Preferential allocation, physio-evolutionary feedbacks, and the stability and
551 environmental patterns of mutualism between plants and their root symbionts. *New Phytolo-
552 gist*, 205:1503–1514.
- 553 Blanquart, F., O. Kaltz, S. L. Nuismer, and S. Gandon. 2013. A practical guide to measuring local
554 adaptation. *Ecology Letters*, 16:1195–1205.
- 555 Bronstein, J. L.. 1994. Conditional outcomes in mutualistic interactions. *Trends in Ecology &
556 Evolution*, 9:214–217.
- 557 Bronstein, J. L.. 2009. The evolution of facilitation and mutualism. *Journal of Ecology*, 97:1160–
558 1170.
- 559 Brooker, R. W. and T. V. Callaghan. 1998. The balance between positive and negative plant inter-
560 actions and its relationship to environmental gradients: a model. *Oikos*, pages 196–207.
- 561 Brown, C. D. and M. Vellend. 2014. Non-climatic constraints on upper elevational plant range
562 expansion under climate change. *Proceedings of the Royal Society of London B: Biological
563 Sciences*, 281:20141779.
- 564 Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: Size, shape,
565 boundaries, and internal structure. *Annual Review of Ecology and Systematics*, 27:pp. 597–
566 623.
- 567 Chamberlain, S. A., J. L. Bronstein, and J. A. Rudgers. 2014. How context dependent are species
568 interactions? *Ecology Letters*, 17:881–890.
- 569 Cushman, J. H. and T. G. Whitham. 1989. Conditional mutualism in a membracid-ant associa-
570 tion: temporal, age-specific, and density-dependent effects. *Ecology*, 70:1040–1047.
- 571 Daleo, P. and O. Iribarne. 2009. Beyond competition: the stress-gradient hypothesis tested in
572 plant-herbivore interactions. *Ecology*, 90:2368–2374.
- 573 Dangles, O., M. Herrera, and F. Anthelme. 2013. Experimental support of the stress-gradient
574 hypothesis in herbivore–herbivore interactions. *New Phytologist*, 197:405–408.

- 575 D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire
576 cycle, and global change. *Annual Review of Ecology, Evolution, and Systematics*, 23:63–87.
- 577 Decaestecker, E., S. Gaba, J. A. M. Raeymaekers, R. Stoks, L. V. Kerckhoven, D. Ebert, and
578 L. D. Meester. 2007. Host–parasite ‘red queen’ dynamics archived in pond sediment. *Nature*,
579 450:870–873.
- 580 Dybdahl, M. F. and C. M. Lively. 1998. Host-parasite coevolution: Evidence for rare advantage
581 and time-lagged selection in a natural population. *Evolution*, 52:1057.
- 582 Eaton, C. J., P.-Y. Dupont, P. Solomon, W. Clayton, B. Scott, and M. P. Cox. 2015. A core gene
583 set describes the molecular basis of mutualism and antagonism in epichloë spp. *Molecular*
584 *Plant-Microbe Interactions*, 28:218–231.
- 585 Espeland, E. and K. Rice. 2007. Facilitation across stress gradients: the importance of local adap-
586 tation. *Ecology*, 88:2404–2409.
- 587 Frederickson, M. E.. 2013. Rethinking mutualism stability: Cheaters and the evolution of sanc-
588 tions. *The Quarterly Review of Biology*, 88:269–295.
- 589 Fugère, V., P. Andino, R. Espinosa, F. Anthelme, D. Jacobsen, and O. Dangles. 2012. Testing the
590 stress-gradient hypothesis with aquatic detritivorous invertebrates: insights for biodiversity-
591 ecosystem functioning research. *Journal of Animal Ecology*, 81:1259–1267.
- 592 Gandon, S., A. Buckling, E. Decaestecker, and T. Day. 2008. Host–parasite coevolution and pat-
593 terns of adaptation across time and space. *Journal of evolutionary biology*, 21:1861–1866.
- 594 Gandon, S. and Y. Michalakis. 2002. Local adaptation, evolutionary potential and host–parasite
595 coevolution: interactions between migration, mutation, population size and generation time.
596 *Journal of Evolutionary Biology*, 15:451–462.
- 597 Haig, D. and M. Westoby. 1988. On limits to seed production. *The American Naturalist*,
598 131:757–759.
- 599 Hanifin, C. T., E. D. Brodie, and E. D. B. III. 2008. Phenotypic mismatches reveal escape from
600 arms-race coevolution. *PLoS Biology*, 6:e60.
- 601 Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are species range limits simply niche
602 limits writ large? a review of transplant experiments beyond the range. *The American Natural-*
603 *ist*, 183:157–173.
- 604 He, Q. and M. D. Bertness. 2014. Extreme stresses, niches, and positive species interactions
605 along stress gradients. *Ecology*, 95:1437–1443.
- 606 He, Q., M. D. Bertness, and A. H. Altieri. 2013. Global shifts towards positive species interac-
607 tions with increasing environmental stress. *Ecology Letters*, 16:695–706.
- 608 HilleRisLambers, J., M. A. Harsch, A. K. Ettinger, K. R. Ford, and E. J. Theobald. 2013. How
609 will biotic interactions influence climate changeinduced range shifts? *Annals of the New York*
610 *Academy of Sciences*, 1297:112–125.

- 611 Hiltner, L.. 1904. Uber neue erfahrungen und probleme auf dem gebeit der bodenbackteriologie
612 und unter besonderer berucksichtigung der grundungung und brache. Arb. Deut. Landwirsch
613 Ges., 98:5978.
- 614 Hochberg, M. E. and M. van Baalen. 1998. Antagonistic coevolution over productivity gradients.
615 The American Naturalist, 152:620–634.
- 616 Hoegh-Guldberg, O.. 1999. Climate change, coral bleaching and the future of the world’s coral
617 reefs. Marine and Freshwater Research, 50:839.
- 618 Hoek, T. A., K. Axelrod, T. Biancalani, E. A. Yurtsev, J. Liu, and J. Gore. 2016. Resource avail-
619 ability modulates the cooperative and competitive nature of a microbial cross-feeding mutual-
620 ism. PLOS Biology, 14:e1002540.
- 621 Holding, M. L., J. E. Biardi, and H. L. Gibbs. 2016. Coevolution of venom function and venom
622 resistance in a rattlesnake predator and its squirrel prey. Proceedings of the Royal Society B:
623 Biological Sciences, 283:20152841.
- 624 Holmgren, M. and M. Scheffer. 2010. Strong facilitation in mild environments: the stress gradi-
625 ent hypothesis revisited. Journal of Ecology, 98:1269–1275.
- 626 Johnson, N. C.. 1993. Can fertilization of soil select less mutualistic mycorrhizae? Ecological
627 Applications, 3:749–757.
- 628 Johnson, N. C., G. W. T. Wilson, M. A. Bowker, J. A. Wilson, and R. M. Miller. 2010. Resource
629 limitation is a driver of local adaptation in mycorrhizal symbioses. Proceedings of the National
630 Academy of Sciences, 107:2093–2098.
- 631 Jones, E. I., M. E. Afkhami, E. Akçay, J. L. Bronstein, R. Bshary, M. E. Frederickson, and *et al.*.
632 2015. Cheaters must prosper: reconciling theoretical and empirical perspectives on cheating in
633 mutualism. Ecology Letters, 18:1270–1284.
- 634 Kardol, P., R. Jonathan, and D. A. Wardle. 2014. Local plant adaptation across a subarctic eleva-
635 tional gradient. Royal Society Open Science, 1:140141.
- 636 Kawakita, A., T. Okamoto, R. Goto, and M. Kato. 2010. Mutualism favours higher host speci-
637 ficity than does antagonism in plant-herbivore interaction. Proceedings of the Royal Society B:
638 Biological Sciences, 277:2765–2774.
- 639 Kawecki, T. J. and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters,
640 7:1225–1241.
- 641 Kettlewell, H. B. D.. 1955. Selection experiments on industrial melanism in the lepidoptera.
642 Heredity, 9:323–342.
- 643 Kiers, E. T. and M. G. van der Heijden. 2006. Mutualistic stability in the arbuscular mycorrhizal
644 symbiosis: exploring hypotheses of evolutionary cooperation. Ecology, 87:1627–1636.

- 645 Klinger, C. R., J. A. Lau, and K. D. Heath. 2016. Ecological genomics of mutualism de-
646 cline in nitrogen-fixing bacteria. *Proceedings of the Royal Society B: Biological Sciences*,
647 283:20152563.
- 648 Lau, J. A. and J. T. Lennon. 2012. Rapid responses of soil microorganisms improve plant fitness
649 in novel environments. *Proceedings of the National Academy of Sciences*, 109:14058–14062.
- 650 Liancourt, P., L. A. Spence, D. S. Song, A. Lkhagva, A. Sharkhuu, B. Boldgiv, and *et al.*. 2013.
651 Plant response to climate change varies with topography, interactions with neighbors, and eco-
652 type. *Ecology*, 94:444–453.
- 653 Liancourt, P. and K. Tielbörger. 2009. Competition and a short growing season lead to ecotypic
654 differentiation at the two extremes of the ecological range. *Functional Ecology*, 23:397–404.
- 655 Lively, C. M. and M. F. Dybdahl. 2000. Parasite adaptation to locally common host genotypes.
656 *Nature*, 405:679–681.
- 657 Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient
658 hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, 97:199–
659 205.
- 660 Malkinson, D. and K. Tielbörger. 2010. What does the stress-gradient hypothesis predict? resolv-
661 ing the discrepancies. *Oikos*, 119:1546–1552.
- 662 Maron, J. L., K. C. Baer, and A. L. Angert. 2014. Disentangling the drivers of context-dependent
663 plant-animal interactions. *Journal of Ecology*, 102:1485–1496.
- 664 Martin, T. E.. 1998. Are microhabitat preferences of coexisting species under selection and adap-
665 tive? *Ecology*, 79:656–670.
- 666 Michalet, R., L. Bagousse-Pinguet, J.-P. Maalouf, C. J. Lortie, et al.. 2014. Two alternatives
667 to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch
668 from facilitation to competition. *Journal of Vegetation Science*, 25:609–613.
- 669 Michalet, R., R. W. Brooker, L. A. Cavieres, Z. Kikvidze, C. J. Lortie, F. I. Pugnaire, A. Valiente-
670 Banuet, and R. M. Callaway. 2006. Do biotic interactions shape both sides of the humped-back
671 model of species richness in plant communities? *Ecology letters*, 9:767–773.
- 672 Michalet, R., S. Xiao, B. Touzard, D. S. Smith, L. A. Cavieres, R. M. Callaway, and T. G.
673 Whitham. 2011. Phenotypic variation in nurse traits and community feedbacks define an alpine
674 community. *Ecology Letters*, 14:433–443.
- 675 Moran, N. A.. 2001. The coevolution of bacterial endosymbionts and phloem-feeding insects.
676 *Annals of the Missouri Botanical Garden*, pages 35–44.
- 677 Nuismer, S. L.. 2006. Parasite local adaptation in a geographic mosaic. *Evolution*, 60:24–30.
- 678 Nuismer, S. L., J. N. Thompson, and R. Gomulkiewicz. 2000. Coevolutionary clines across selec-
679 tion mosaics. *Evolution*, 54:1102–1115.

- 680 Pachauri, R. K., M. R. Allen, V. R. Barros, J. Broome, W. Cramer, R. Christ, J. A. Church,
681 L. Clarke, Q. Dahe, P. Dasgupta, et al.. 2014. *Climate change 2014: synthesis report. Con-*
682 *tribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental*
683 *Panel on Climate Change*. IPCC.
- 684 Parker, M. A.. 1999. Mutualism in metapopulations of legumes and rhizobia. *The American*
685 *Naturalist*, 153:S48–S60.
- 686 Pascua, L. L., S. Gandon, and A. Buckling. 2011. Abiotic heterogeneity drives parasite local
687 adaptation in coevolving bacteria and phages. *Journal of Evolutionary Biology*, 25:187–195.
- 688 Paterson, S., T. Vogwill, A. Buckling, R. Benmayor, A. J. Spiers, N. R. Thomson, and *et al.*
689 2010. Antagonistic coevolution accelerates molecular evolution. *Nature*, 464:275–278.
- 690 Pfennig, K. and D. Pfennig. 2009. Character displacement: ecological and reproductive responses
691 to a common evolutionary problem. *The Quarterly Review of Biology*, 84:253–276.
- 692 Pringle, E. G., E. Akçay, T. K. Raab, R. Dirzo, and D. M. Gordon. 2013. Water stress strengthens
693 mutualism among ants, trees, and scale insects. *PLoS Biology*, 11:e1001705.
- 694 Revillini, D., C. A. Gehring, and N. C. Johnson. 2016. The role of locally adapted mycorrhizas
695 and rhizobacteria in plant-soil feedback systems. *Functional Ecology*, 30:1086–1098.
- 696 Rúa, M. A., A. Antoninka, P. M. Antunes, V. B. Chaudhary, C. Gehring, L. J. Lamit, and *et al.*
697 2016. Home-field advantage? evidence of local adaptation among plants, soil, and arbuscular
698 mycorrhizal fungi through meta-analysis. *BMC Evol Biol*, 16.
- 699 Rubin, B. E. R. and C. S. Moreau. 2016. Comparative genomics reveals convergent rates of evo-
700 lution in ant–plant mutualisms. *Nature Communications*, 7:12679.
- 701 Sachs, J. L., U. G. Mueller, T. P. Wilcox, and J. J. Bull. 2004. The evolution of cooperation. *The*
702 *Quarterly Review of Biology*, 79:135–160.
- 703 Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a lat-
704 itudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolu-*
705 *tion, and Systematics*, 40:245–269.
- 706 Schöb, C., R. M. Callaway, F. Anthelme, R. W. Brooker, L. A. Cavieres, Z. Kikvidze, C. J. Lortie,
707 R. Michalet, F. I. Pugnaire, S. Xiao, et al.. 2014a. The context dependence of beneficiary
708 feedback effects on benefactors in plant facilitation. *New Phytologist*, 204:386–396.
- 709 Schöb, C., R. Michalet, L. A. Cavieres, F. I. Pugnaire, R. W. Brooker, B. J. Butterfield, B. J.
710 Cook, Z. Kikvidze, C. J. Lortie, S. Xiao, et al.. 2014b. A global analysis of bidirectional in-
711 teractions in alpine plant communities shows facilitators experiencing strong reciprocal fitness
712 costs. *New Phytologist*, 202:95–105.
- 713 Schwartz, M. W. and J. D. Hoeksema. 1998. Specialization and resource trade: biological mar-
714 kets as a model of mutualisms. *Ecology*, 79:1029–1038.

- 715 Sexton, J. P., M. B. Hufford, A. C. Bateman, D. B. Lowry, H. Meimberg, S. Y. Strauss, and K. J.
716 Rice. 2016. Climate structures genetic variation across a species' elevation range: a test of
717 range limits hypotheses. *Molecular Ecology*, 25:911–928.
- 718 Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species
719 range limits. *Annual Review of Ecology, Evolution, and Systematics*, 40:415–436.
- 720 Smith, S. E., E. Facelli, S. Pope, and F. A. Smith. 2010. Plant performance in stressful environ-
721 ments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas.
722 *Plant and Soil*, 326:3–20.
- 723 Smith, S. E. and D. J. Read. 2008. 3rd edition. *Mycorrhizal symbiosis*. Academic press, London.
- 724 Staskawicz, B. J., F. M. Ausubel, B. J. Baker, J. G. Ellis, and J. D. Jones. 1995. Molecular genet-
725 ics of plant disease resistance. *Science*, 268:661.
- 726 Sthultz, C. M., C. A. Gehring, and T. G. Whitham. 2007. Shifts from competition to facilitation
727 between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid
728 woodland. *New Phytologist*, 173:135–145.
- 729 Stokes, A. N., A. M. Ray, M. W. Buktenica, B. G. Gall, E. Paulson, D. Paulson, and *et al.*. 2015.
730 Otter predation on taricha granulosa and variation in tetrodotoxin levels with elevation. *North-*
731 *western Naturalist*, 96:13–21.
- 732 Stuart, Y. E. and J. B. Losos. 2013. Ecological character displacement: glass half full or half
733 empty? *Trends in Ecology & Evolution*, 28:402–408.
- 734 Thompson, J. N.. 2005. *The geographic mosaic of coevolution*. University of Chicago Press,
735 Chicago.
- 736 Thrall, P. H., M. E. Hochberg, J. J. Burdon, and J. D. Bever. 2007. Coevolution of symbiotic
737 mutualists and parasites in a community context. *Trends in Ecology & Evolution*, 22:120–126.
- 738 Toju, H., H. Abe, S. Ueno, Y. Miyazawa, F. Taniguchi, T. Sota, and T. Yahara. 2011. Climatic
739 gradients of arms race coevolution. *The American Naturalist*, 177:562–573.
- 740 Travis, J., R. Brooker, E. Clark, and C. Dytham. 2006. The distribution of positive and negative
741 species interactions across environmental gradients on a dual-lattice model. *Journal of Theo-*
742 *retical Biology*, 241:896–902.
- 743 van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and
744 abundance responses to climate change: why it is essential to include biotic interactions across
745 trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
746 365:2025–2034.
- 747 Van Valen, L.. 1974. Molecular evolution as predicted by natural selection. *Journal of Molecular*
748 *Evolution*, 3:89–101.
- 749 Wang, T., G. A. O'Neill, and S. N. Aitken. 2010. Integrating environmental and genetic effects to
750 predict responses of tree populations to climate. *Ecological Applications*, 20:153–163.

- 751 Weese, D. J., K. D. Heath, B. Dentinger, and J. A. Lau. 2015. Long-term nitrogen addition causes
752 the evolution of less-cooperative mutualists. *Evolution*, 69:631–642.
- 753 Zhang, Q.-G. and A. Buckling. 2016. Resource-dependent antagonistic coevolution leads to a
754 new paradox of enrichment. *Ecology*, 97:1319–1328.
- 755 Zhu, X.-C., F.-B. Song, and H.-W. Xu. 2009. Arbuscular mycorrhizae improves low temperature
756 stress in maize via alterations in host water status and photosynthesis. *Plant Soil*, 331:129–137.